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Gravity Modulates Behaviour Control Strategy

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Abstract

Human behaviour is a trade-off between exploitation of familiar resources and exploration of new ones. In a challenging environment - such as outer space - making the correct decision is vital. On Earth, gravity is *always there*, and is an important reference for behaviour. Thus altered gravitational signals may affect behaviour control strategies. Here we investigated whether changing the body's orientation to the gravitational vector would modulate the balance between routine and novel behaviour. Participants completed a Random Number Generation task while upright or supine. We found decreased randomness when participants were supine. In particular, the degree of equiprobability of pairs of consecutive responses was reduced in the supine orientation. Online gravitational signals may shape the balance between exploitation and exploration, in favour of more stereotyped and routine responses.

Keywords:

Gravity, Vestibular System, Exploration, Exploitation, Cognition, Behaviour Control.

Introduction

Human behaviour control strategy is a trade-off between exploitation of familiar choices and exploration of new ones (Cohen, McClure, & Yu, 2007). Thus, every behaviour is based on a decision of whether to adopt stereotyped but possibly suboptimal alternatives or to explore novel and potentially more profitable options. Making the correct decision is vital in high-pressured environments, such as space travel, remarked upon by Canadian Astronaut Chris Hadfield: “Most of the time you only really get one try to do most of the critical stuff and the consequences are life or death” (Greig, 2017). During spaceflight, astronauts are in an extremely challenging environment in which decisions must be made quickly and efficiently. To ensure crew well-being and mission success, understanding how cognition is affected by gravity is vital (Strangman, Sipes, & Beven, 2014). Here we show that experimental alterations of gravity produce rapid changes in behavioural control. Our results identify a key role of online gravitational signals in behavioural control strategies, and in particular in shaping the balance between exploration and exploitation.

On Earth, gravity is *always there* and it *never changes*. Although gravitational signals are part of the background of our perceptual world, they play an important role as a reference for behaviour (Jörges & López-moliner, 2017; Lacquaniti et al., 2015). The central nervous system does not have specialised sensors for the detection of gravity. Rather, gravity is inferred through a process termed *graviception*. Vestibular information from the inner ear is particularly important in this process: when the head is upright, the otolith organs continually sense the pull of gravity, signalling to the brain the position of the head with respect to the gravitational direction (Green, Shaikh, & Angelaki, 2005; Merfeld, Zupan, & Peterka, 1999). However, when the head is tilted, the otolith organs are reoriented with respect to the gravitational direction, and do not provide gravity cues (Kaptein & Van Gisbergen, 2006; Vimal, DiZio, & Lackner, 2017). Therefore, an upright or tilted head posture can be used to naturally stimulate the vestibular system.

Similarly, in weightlessness, the otolith organs no longer receive “normal” gravitational input, triggering disturbances such as Space Adaptation Syndrome, and impairments in visuospatial abilities (Macneil, Che, & Khan, 2016; Manzey, Lorenz, Schiewe, Finell, & Thiele, 1993). Interestingly, several

1 studies have suggested changes in decision-making and wider cognition when under conditions
2 mimicking a zero-gravity environment (Lipnicki & Gunga, 2009; Steinberg, Kalicinski, Dalecki, & Bock,
3 2015; Strangman, Sipes, & Beven, 2014). For example, Lipnicki, Gunga, Belavy, and Felsenberg
4 (2009) found that participants undergoing head-down bed rest failed to adapt their strategy during the
5 Iowa Gambling Task, compared to control participants who switched to a more advantageous
6 strategy. Therefore, it is possible that changes in gravity signals may influence behavioural control
7 strategies.

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9 To investigate whether short-term alterations in vestibular-gravitational signals could influence
10 the balance between routine and novel behaviour, we used a standard Random Number Generation
11 paradigm in which participants were asked to generate sequences of numbers as randomly as
12 possible (Loetscher & Brugger, 2007). Random Number Generation involves both suppressing
13 stereotyped responses and generating non-stereotyped responses, and it can be considered a proxy
14 for flexible and adaptive cognition (Daniels, Witt, Wolff, Jansen, & Deuschl, 2003). We reasoned that
15 measures of randomness and redundancy could elucidate participants' behavioural control strategy,
16 in that increased randomness and/or decreased redundancy would indicate 'exploration', while the
17 reverse pattern would correspond with 'exploitation'. Specifically, exploration is related to novelty and
18 generation of new responses, which may accord with the production of random sequences of digits
19 (Bains, 2008).

20
21 Several studies have demonstrated that the Random Number Generation includes a spatial
22 component, corresponding to movement across the non-verbal mental number line. Small numbers
23 are associated with the left side of space, while larger numbers are associated with the right side
24 (Dehaene, 1992). Results indicated a spatial-numerical interaction in random number generation:
25 numbers were spontaneously remapped to spatial locations along a number line (Loetscher & Brugger
26 2007; Strengé & Rogge, 2010). Additionally, participants seem to mentally visualize the order of digits
27 to facilitate the process of number generation (Towse 1998; Towse & Neil, 1998).

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29 We manipulated how the vestibular organs sense gravity by changing the body's orientation
30 to the direction of the gravitational vector. Thus, participants completed the Random Number
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Generation task while either upright or lying supine. In the former condition, the body and vestibular organs are congruent with the direction of gravity, while in the latter they are orthogonal. Thus, this is an efficient lab-manipulation which allows us to reliably mimic vestibular-gravitational alterations, avoiding other non-specific physiological changes. Based on the previous literature on the effect of altered gravity exposure on both perception and cognition (Lipnicki et al., 2009; Macneil et al., 2016), we hypothesised that short-term alterations in vestibular-gravitational signals may modulate randomness measures. We therefore predicted a decrease randomness in the supine body orientation.

Methods

Ethics

The experimental protocol was approved by the local research ethics committee of Royal Holloway, University of London, and the study was completed in line with the Declaration of Helsinki. Written informed consent was obtained from the participants before commencing the experiment.

Participants

Twenty-six participants (25 female, M age = 19.54, SD = 2.21) took part in this study. All participants were right-handed as assessed using the Edinburgh handedness inventory (Oldfield, 1971). Participants with history of neurological, psychiatric or vestibular disorders were excluded. The sample size was a priori decided based on similar psychophysical experiments. The a priori established sample size was also used as data-collection stopping rule, i.e. when 26 participants were administered with the task, no more volunteers have been recruited for this study. Data from each participant were gathered in a single session. One participant was excluded from analysis due to not following task instructions.

Procedure

After completing informed consent procedures, participants were given task instructions and performed a practice sequence of Random Number Generation. Instructions were as follows: *"In this task you are asked to generate a sequence of 20 random digits. You are asked to name the digits from 1 to 9 (1,2,3,4,5,6,7,8,9) as randomly as possible. A training sequence will be performed to let you understand the timing of the experiment. The number generation is paced by a series of tones. The beginning of the sequence is signalled by three different tones which represent a 'ready-steady-go' signal. You have to start the generation of digits after the last tone, i.e. 'go' tone, but in concomitance to the first beat. Try to be accurate with the timing. You will perform the task in both standing and supine postures."*

The Random Number Generation task was based on standard methods (Towse & Neil, 1998). This task requires participants to generate a sequence of 20 consecutive digits (Ferrè, Vagnoni, & Haggard, 2013). While longer durations of number generation are typically used in previous experiments (Towse & Neil, 1998), here we kept the sequences short in order to prevent sensory adaptation in the vestibular signalling, and to ensure that the participants remained comfortable throughout. Participants were instructed to name digits ranging from 1-9 as randomly as possible. Generation was paced at 2Hz by naming the digits in time with auditory cues. The start of the trial was indicated by three different sounds, and participants were instructed to consider them as a 'ready-steady-go' signal and to start the number generation after the 'go' tone but in concomitance to the first beat. Participants completed the task with the eyes closed in all sequences.

Participants completed the Random Number Generation task while upright or supine. To ensure that somatosensory and proprioceptive information was similar across body orientations, participants were instructed to keep the back, head, palms of the hands, arms and heels in contact with the supporting surface. Participants performed three Random Number Generation sequences while upright and three while supine in a counterbalanced order.

Data Analysis

The quality of randomness generated was analysed through calculation of the Random Number Generation Index (RNG-I). The RNG-I assesses the degree of equiprobability of pairs of consecutive responses and ranges from 0 (all sequential pairs equally frequent) to 1 (perfect predictability of a digit from the preceding digit). Higher values of RNG-I therefore correspond to stereotyped responses, or increased exploitation, while lower values reflect less stereotypy, or increased exploration.

The Redundancy Score (*R* Score) was also applied to estimate the sampling bias by identifying the deviations from the equiprobability of response alternatives. *R* score ranges from 0 (all alternatives generated equally frequently) to 100 (one single alternative provided on all trials) (Towse & Neil 1998). Low *R* Score values correspond to novel behaviour or exploration, and high values to routine behaviour or exploitation.

To assess the spatial component of random number generation, the percentage of large digits (≥ 6) was calculated, indicating preference for the right of the number line. First order differences (FODs) indicated an ascending (positive differences) or descending (negative differences) series, following the right or left of the number line respectively. Repetition of numbers and counting could also be assessed through FODs.

An open-source program was used to calculate *R* Score and RNG-I (<http://www.lancs.ac.uk/staff/towse/rqcpage.html>). For all variables, scores were generated for each sequence and these scores were averaged across conditions (i.e. the average of three scores while upright and three while supine) to produce one value per condition per participant for the overall analysis. Differences between upright and supine conditions were assessed by paired *t*-tests. Bayes Factors were calculated in JASP version 0.8.1.2 (JASP Team, 2018) for each dependent variable. The default Cauchy prior distribution with a scale factor of 0.707 was used to calculate Bayes factors.

Results

Means and standard deviations for each dependent variable can be seen in Table 1.

*** Please insert Table 1 about here ***

Orientation of the body with respect to gravity had a significant effect on RNG-I scores, with a higher RNG-I score for the supine, gravity incongruent, ($M = 0.25$, $SD = 0.09$) relative to upright, gravity congruent, ($M = 0.18$, $SD = 0.08$) condition ($t(24) = -3.12$, $p = .005$, Cohen's $d = 0.624$, 95% CI $[-0.12, -0.02]$, $BF = 9.18$) (Figure 1A). This indicated that randomness was decreased when participants were supine compared to when they were upright. This may therefore correspond to decreased exploration when the body is no longer aligned with the direction of gravity. No significant effect of body orientation was found on R score ($t(24) = -2.01$, $p = .056$, Cohen's $d = 0.40$, 95% CI $[-2.67, 0.04]$, $BF = 1.18$) (Figure 1B).

*** Please insert Fig. 1 about here***

Body orientation with respect to gravity elicited a significant difference in the percentage of large digits produced ($t(24) = 2.55$, $p = .018$, 95% CI $[0.64, 6.10]$, Cohen's $d = 0.51$, $BF = 2.98$), with a smaller percentage of large digits produced when participants were supine relative to upright. However, no significant differences were found in either positive ($t(24) = 0.57$, $p = .571$, Cohen's $d = 0.12$, 95% CI $[-0.45, 0.80]$, $BF = 0.25$) or negative FODs ($t(24) = 1.36$, $p = .19$, Cohen's $d = 0.27$, 95% CI $[-0.22, 1.04]$, $BF = 0.48$).

Discussion

Deep space exploration is no longer a distant future, with several space agencies and private companies aiming for manned missions to Mars within the coming decades (Wickman, 2006; Wilson, 2017). One of the most significant challenges is the maintenance of the crew's health and physical fitness. Exposure to non-terrestrial gravity environments leads to several changes in the human body (Macneil et al., 2016; Manzey et al., 1993). Surprisingly, the role of gravity on behaviour control strategy has not yet been investigated. Given the technical and communication limitations in space environments, knowing the consequences of altered gravitational signals on how people take decisions is essential.

Behaviour control strategy often involves trade-off between exploiting old solutions and exploring new ones (Cohen et al., 2007; Daw, O'Doherty, Dayan, Seymour, & Dolan, 2006; Sugrue, Corrado, & Newsome, 2004). A generative task, like Random Number Generation, involves the decision of whether to exploit (i.e. to repeat the same digits) or to explore (i.e. to name new digits). Here we investigated whether short-term changes in gravitational signalling on the basis of tilting the body away from the gravitational acceleration might affect randomness in a Random Number Generation task. Results indicated that people were less prone to generating random behaviours while supine relative to upright. Thus, online gravitational signals may shape the balance between exploitation and exploration, in favour of more stereotyped and routine responses. The contribution of gravitational signals to this fundamental aspect of cognition may have been overlooked simply because gravitational signals are ubiquitous, and normally invariant.

To assess the quality of randomness generated we estimated the Random Number Generation Index (RNG-I, i.e. the degree of equiprobability of pairs of consecutive responses) and the Redundancy Score (*R* Score, i.e. the deviation from the equiprobability of response alternatives). Interestingly, while we found a significant difference between RNG-I when supine relative to upright, Redundancy Scores were similar across body orientations. Although Towse and Neil's (1998) factor analysis found that these measures are both loaded on the Equality of Response Usage factor,

important distinctions between the two measures exist. Specifically, as previously mentioned, RNG-I reflects the predictability of response pairs, while R-scores instead assess the use of response alternatives. Thus, while RNG scores assess randomness across the entire sequence, R-scores reflect a more general sampling bias (Sexton & Cooper, 2014). It is therefore possible that an overall change in vestibular-gravitational signalling may affect one component over the other.

Previous studies have found links between vestibular signalling and changes in random number generation behaviour. For example, Moser, Vibert, Caversaccio, and Mast (2017) found that patients with peripheral vestibular deficits showed decreased randomness during random number generation, suggesting impairments in executive functioning. Moreover, Ferrè et al. (2013) found that left-anodal/right-cathodal galvanic vestibular stimulation increased the randomness of generated sequences, while the reverse polarity namely right-anodal/left-cathodal galvanic vestibular stimulation decreased randomness. Goldberg, Podell, and Lovell (1994) suggested that right hemisphere activation is necessary for exploratory processing, while the left hemisphere is related to exploitation of routine behaviours. Thus, the polarity differences found by Ferrè et al. (2013) may reflect differential hemispheric activations. In the present study, we utilised natural vestibular stimulation, and thus we are unable to assess hemispheric differences. Our findings may reflect an overall change in vestibular processing due to the alteration of vestibular-gravitational cues.

Our results suggests a gravitational bias on the spatial distribution of numbers. The random number generation task has been previously adopted to investigate the properties of the non-verbal mental number line (Loetscher & Brugger 2007; Strengé & Rogge, 2010). Loetscher, Schwarz, Schubiger and Brugger (2008) found that actively turning the head to the left or right biased participants' responses towards smaller or larger numbers respectively. Similarly, Hartmann, Grabherr, and Mast (2012) have shown that passive whole-body movements leftwards and downwards induced a bias towards smaller numbers, while rightwards and upwards movements caused biases towards larger numbers. Here we observed an overall tendency to produce smaller than larger numbers. We also found that participants produced even smaller numbers when supine relative to upright. Thus, changes in body orientation relative to gravity may also influence spatial

1 attention to the number line. However, we cannot exclude that the bias in reporting small numbers
2 may itself influences randomness. While spatial component and randomness measures of random
3 number generation assess different underlying constructs (Towse & Neil, 1998; Loetscher & Brugger
4 2007), their estimates may not be entirely independent: a bias in the spatial component – as the small
5 number bias observed – could limit the number of possible response pairs, resulting in reduced
6 randomness.
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14 Relatively short sequences of numbers were used in the Random Number Generation task.
15 This sequence length was chosen first to avoid vestibular habituation to the body orientation during
16 sequence generation, and second to avoid participants experiencing discomfort should they have to
17 maintain a fixed body orientation for a long period of time. However, we cannot exclude that longer
18 sequences may yield different results, potentially limiting the findings of our study. In particular, longer
19 sequences may allow the opportunity for participants to present more response alternatives, changing
20 the overall randomness of the sequence. Variation is present in sequence length and digit range
21 across the random number generation literature, with participants producing as many as 100 (Towse,
22 Towse, Saito, & Maehara, 2016) or as few as 20 digits (Ferrè et al., 2013) across different studies.
23 As such, the ‘optimal’ sequence length for Random Number Generation is unknown. Overall, the
24 absolute values of randomness are perhaps less pertinent to the present study than the observed
25 changes between upright and supine body orientation conditions.
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41 The balance between novel and routine behaviour is fundamental to successfully interact with
42 the external environment. On Earth, gravity is a signal which is ever-present, and acts as a reference
43 for behaviour. Here we found that short-term alterations in vestibular-gravitational signals changed
44 participants’ random number generation behaviour, with increased exploitation when supine. Thus,
45 our findings suggest that gravitational inputs may influence behavioural control strategies.
46 Importantly, we note that more drastic changes in gravitational signalling, such as exposure to
47 weightlessness in space-flight, may have different effects on behavioural control than our
48 manipulation. At present the effects of altered gravity on behavioural control are unknown, and require
49 further research.
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Author Contributions

I.A. performed experiments; M.G., I.A. and E.R.F. analysed data; E.R.F. conception and design of research; E.R.F., M.G. and I.A. interpreted results of experiments; E.R.F. and M.G. edited and revised manuscript; all authors approved final version of manuscript.

Conflict of interest

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Figure Legend

Figure 1. Randomness and redundancy results in each experimental conditions.

Participants performed a number generation in which they were asked to generate sequences of 20 consecutive digits ranging from 1-9 as randomly as possible. Generation was paced at 2Hz by naming the digits in time with auditory cues. Vestibular information was manipulated altering the natural position of the body – and therefore of the otolith organs – with respect to gravity. Participants completed the random number generation task while upright, i.e. congruent with gravitational direction, and supine, i.e. orthogonal to gravitational direction. Box-and-whisker plots comparing the effect of body orientation for randomness and redundancy scores. The upper and lower bound of each box represent the 75th and 25th percentiles of the distribution, and the median is represented by the thick horizontal line inside the box. The top and bottom ends of the whisker represent the 95th and 5th percentiles of the distribution, respectively. Dots represent outliers. Orientation of the body with respect to gravity had a significant effect on randomness (A). The RNG-I score is higher for the supine condition relative to upright condition. Redundancy score (R-Score) did not show significant changes (B).

Gravity Modulates Behaviour Control Strategy
Gallagher, Arshad, Ferrè

Table 1. Means and SDs for each dependent variable.

	Standing	Supine
	Mean (SD)	Mean (SD)
Large Digits (%)	45.88 (6.70)	42.51 (6.35)
Positive FODs	9.65 (1.10)	9.48 (1.51)
Negative FODs	8.01 (1.29)	7.60 (1.56)
R	4.31 (2.02)	5.63 (2.94)
RNG-I	0.18 (0.08)	0.25 (0.09)

